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The Kidney, Adrenocortical Homolog, and Corpuscles of Stannius in the Cockscomb Prickleback *Anoplarchus purpurescens*

John H. Youson, David G. Butler and Kanella Tsioros

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Abstract The morphology of the kidney, adrenocortical homolog, and the corpuscles of Stannius was examined in the cockscomb prickleback, *Anoplarchus purpurescens*, a marine teleost which inhabits the intertidal zone. The paired kidneys of this fish are fused throughout most of their length, there is essentially a single posterior cardinal vein on the right side, they possess renal corpuscles, and there is no distal segment of the tubule. The tubule is specialized, in descending order, into ciliated neck and two proximal segments before entering the system of collecting tubules and ducts. The cells of the latter system are specialized for mucous secretion, as are cells of the main excretory ducts, the paired archinephric ducts. Tubulogenesis occurs in the kidneys in close apposition to the archinephric ducts. The presumptive adrenocortical homolog is located around the posterior cardinal veins in the head kidney while paired corpuscles of Stannius are confined to the posterior end of the kidney. All of the above features are consistent with those found in the kidneys of many other marine teleosts.

The morphology of the kidney of each species of teleost often reflects the osmotic demands placed on the organism by the environment (Hickman and Trump, 1969). Thus, the freshwater fishes are faced with the need to produce copious amounts of a dilute urine and, therefore, their kidneys have well developed renal corpuscles and both proximal and distal segments in the tubules (Hentschel and Elger, 1987). In contrast, marine fishes have to conserve water and produce small amounts of concentrated urine and consequently their kidneys are either aglomerular (no renal corpuscles) or with poorly developed renal corpuscles. Frequently, the kidneys of marine teleosts also have an extensive proximal segment and little or no distal segment in the tubules. Additional components of the kidneys which may have some bearing on the ability of fishes to osmoregulate are two different types of endocrine tissue: the adrenocortical homolog or interrenal tissue and the corpuscles of Stannius (Krishnamurthy and Bern, 1969; Butler, 1973). The presence or absence of the corpuscles of Stannius and the distribution of the adrenocortical homolog are important considerations in the evaluation of the functional-morphology of fish kidneys.

We have been examining the morphology of the renal tissue and the distribution of the adrenocortical homolog and the corpuscles of Stannius in kidneys of bony fishes considered to be more primitive than teleosts (for review, see Youson and Butler, 1988; Youson et al., 1988). The kidneys of these primitive freshwater fishes show some marked differences in renal morphology and distribution of adrenocortical tissue and corpuscles of Stannius to that presently described for more advanced marine and freshwater teleosts (Youson and Butler, 1976; Youson et al., 1976; Youson and Butler, 1988). The next step in our research program was to examine the kidney from a teleost, but we wished to examine a species in which there had been no prior description and one which might show marked differences from those presently described. We chose the blenny family and in particular the cockscomb prickleback *Anoplarchus purpurescens* Gill. This species, distributed from Northern California to the Bering Sea, is usually located under rocks in the intertidal zone and is probably subjected to varying salinity in shallow tide pools as the result of evaporation and by dilution with rainwater. There has been only brief mention of the kidney of Blennidae (Ogawa, 1962; Hickman and Trump, 1969). In the present study we use light microscopy to describe the morphology of the kidney and the distribution of both the adrenocortical homolog and the corpuscles of Stannius of *A.*

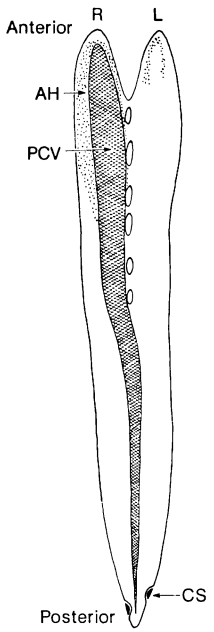

Fig. 1. Diagrammatic representation of the kidney of *Anoplarchus purpurescens* showing right (R) and left (L) kidneys fused throughout most of their length, the posterior cardinal vein (PCV), and the distribution of the adrenocortical homolog (AH) and the corpuscles of Stannius (CS).

purpurescens.

Materials and methods

Anoplarchus purpurescens 5.5–7.8 cm long, were collected in the tide pools of the Strait of Georgia, near Vancouver, British Columbia, Canada. Following a small incision in the abdomen, the animals were fixed in toto in Bouin's fluid for 24 hrs. and then were stored in 70% ethanol until used. The entire abdominal region from near the heart to the cloaca was cut into numbered segments and each segment was embedded separately in paraffin following routine procedures. Tissue blocks were cut at 10 μm and the serial sections from 3 animals were placed on glass slides. The slides were stained alternately with either periodic acid-Schiff, haematoxylin, and orange G or with haematoxylin and eosin.

Results

General morphology. The paired, opisthonephric kidneys were situated in the dorsal wall of the coelomic cavity and were directly apposed to the great dorsal vessels (posterior cardinal veins, dorsal aorta) and the vertebral column (Figs. 1, 2a). Laterally they were surrounded by the musculature of the body wall. The kidneys extended from just posterior to the pericardium to the cloaca. Throughout approximately the anterior one-fifth of their length the kidneys were widely separated by muscle tissue as two slender elements (Fig. 2a) but subsequently they fused and separated several times at their mid-point (perhaps reflecting their intimacy with vertebrae) after which they extended to the cloaca as a single mass of renal tissue (Figs. 1, 2b–d). A single posterior cardinal vein extended almost entirely throughout the length of the kidneys occupying the majority of the right kidney in the anterior one-half but eventually gradually tapering in size while taking up a central position in the fused kidneys to the cloaca (Figs. 1, 3). A renal portal vein originated from the caudal vein in the posterior part of the coelomic cavity and was seen in the fused kidneys as far up as their midpoint (Fig. 3).

Transverse sections revealed that the kidneys were of variable shape throughout their length and this shape reflected their periodic fusion and the location of the posterior cardinal in the anterior region and their permanent fusion in the posterior region (Figs. 2a–d, 3). Thus, although the anterior part of the fused kidney was like a broad ribbon (Fig. 2b), most of the posterior one-half was vase-shaped with the dorso-lateral sides invaginated (Figs. 2d, 3). Haemopoietic tissue was present throughout the kidneys but it was the primary component in the most anterior region (Figs. 2b, c). Thereafter there was an almost equal distribution of haemopoietic and renal tissue (Fig. 2d).

Endocrine tissue. The presumptive adrenocortical tissue (PAT) appeared as cords of pale staining epithelial cells and extended over one-quarter to one-third the length of the right kidney but only one-tenth to one-fifth the length of the left kidney. The more extensive distribution of PAT in the right kidney was undoubtedly due to the location of the posterior cardinal vein in this kidney, for there was always an intimate relationship between the pale cells and blood vessels (Fig. 4a). The cords of cells were not encapsulated

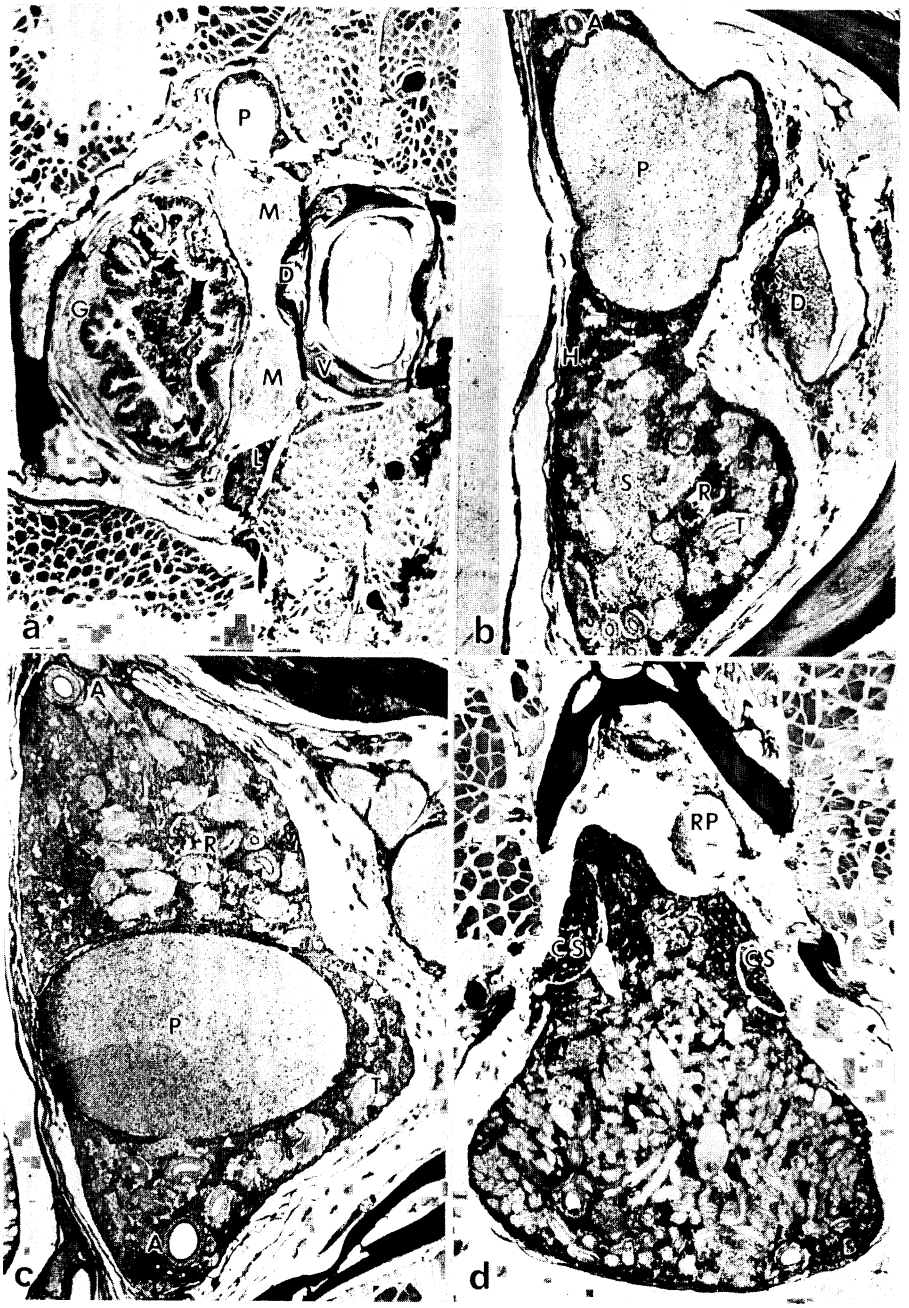

Fig. 2. The kidney of *Anoplarchus purpurescens* at various sites in the coelomic cavity. a: In the most anterior region, the right kidney with large posterior cardinal vein (P) and the left kidney (L) are separated by muscle (M) and are located below the vertebral column (V) and dorsal aorta (D). G, gut. ×25. b: Anterior part shortly after initial fusion of kidneys showing large posterior cardinal vein (P) and archinephric duct (A) in right kidney and a smaller vein (S), renal tubules (T), renal corpuscles (R), and much haemopoietic tissue (H) in the left. D, dorsal aorta. ×100. c: Middle part with posterior cardinal vein (P) in approximate centre of the fused kidneys each of which possess an archinephric duct (A), tubules (T), and renal corpuscle (R). ×100. d: In the most posterior part the vase-shaped kidneys possess the two corpuscles of Stannius (CS). RP, renal portal vein. ×40.

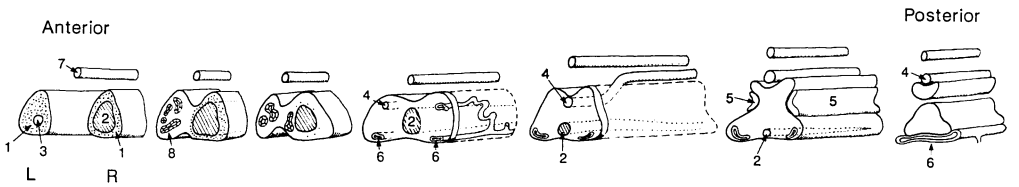

Fig. 3. Diagrammatic representations of the separate and fused right (R) and left (L) kidneys of *Anoplarchus purpurescens* at seven regions from their anterior to posterior end. Included are the adrenocortical homolog (1), the large right (2) and small left (3) posterior cardinal veins, the caudal and renal portal veins (4), the corpuscles of Stannius (5), the archinephric ducts (6), the dorsal aorta (7), and the renal tubules (8).

or even grouped into distinct corpuscles but instead were usually seen diffusely distributed around the posterior cardinal and renal veins. The cords were separated by an extensive network of sinusoids and their cells possessed a vacuolated cytoplasm and a spherical nucleus with prominent nucleolus. The cytoplasm showed no staining with periodic acid-Schiff.

We made no attempt to identify cells which were homologous to the adrenal medullary tissue of higher vertebrates. Positive identification of this so called "chromaffin tissue" requires different fixation (e.g. potassium dichromate) under a chromaffin reaction. However, with our fixation and staining techniques it was possible to recognize cells scattered randomly among the PAT which stained more intensely with haemotoxylin. We could only tentatively identify these cells as chromaffin cells.

An oval-shaped body was located on each dorsolateral surface of the vase-shaped, fused kidney in its most posterior region (Figs. 1, 2d). Each body corresponded to a corpuscle of Stannius (CS). The position of these 2 CS had no bearing on the location of large vessels, as was the case with PAT, but veins of moderate size were usually nearby. The CS were between 300–600 μm in length but they were approximately of equal size in each individual animal. Examination of serial sections in an anterio-posterior direction indicated that the CS did not appear directly opposite one another but there was no consistency as to which side of the fused kidneys first possessed a CS (Fig. 1). In one animal, the CS on the left side appeared 500 μm before the other. Consequently, most transverse sections of the posterior kidney region showed two CS of unequal dimension or just one CS (Fig. 2d).

The CS had a distinctly different histological appearance from the PAT. Each CS was composed of branched and anastomosing cords of epithelial cells which were separated by wide sinusoids and clearly delineated from the surrounding haemopoietic tissue by what appeared to be a thin capsule of fibrous connective tissue (Fig. 4b). The cells contained spherical nuclei and their cytoplasm was basophilic with haemotoxylin and eosin and contained granules which stained positively with periodic acid-Schiff (Fig. 4b).

Renal tissue. Only the anterior 200–300 μm of the kidney was free of renal tissue. The remainder contained tubules, renal corpuscles, and the archinephric (urinary) ducts among the haemopoietic tissue (Figs. 2b–d). The nephrons, the fundamental units of the kidney, were each composed of a renal corpuscle and a tubule subdivided into segments (Fig. 5). A short ciliated neck segment extended from the renal corpuscle and lead into proximal segment I which inturn was continuous with proximal segment II. Collecting tubules received one or more nephrons before entering a short collecting duct which extended into the archinephric duct. There was a single archinephric duct for each kidney, or for each side of the fused kidney (Fig. 2c), but they united before entering the cloaca.

Renal corpuscle: For the most part the renal corpuscles were randomly distributed in the kidneys, however, there appeared to be a tendency for them to be located in small groups and in close proximity to the archinephric duct (Fig. 4c). Each corpuscle consisted of a central glomerulus surrounded by a double-layered, Bowman' capsule (Fig. 4d). The capillaries of the glomerulus were supplied by an afferent arteriole and were drained by an efferent arteriole both of which could be visualized at the vascular pole (Fig. 4d). The inner layer of Bowman's capsule, the visceral

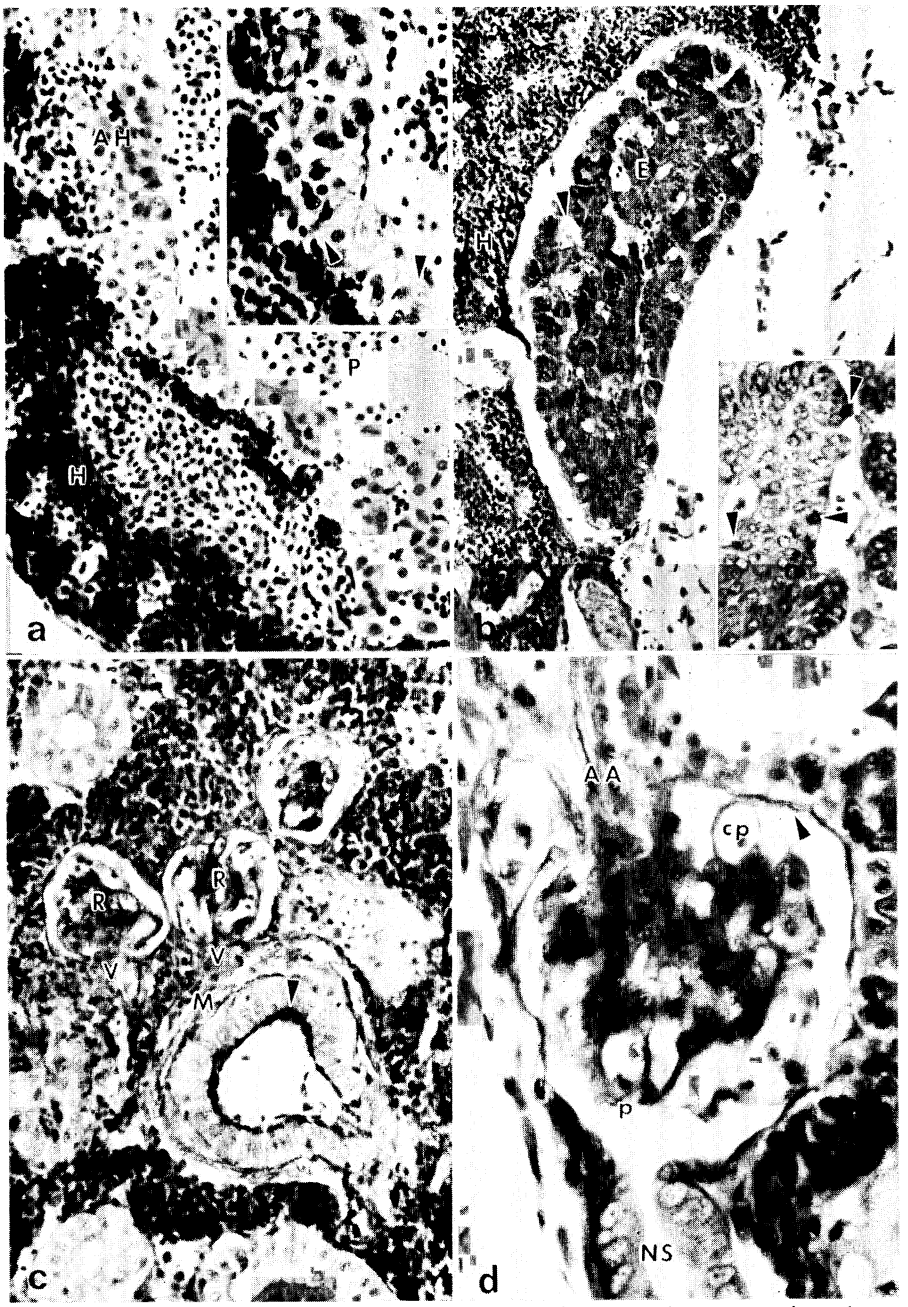

Fig. 4. The kidney of *Anoplarchus purpurescens* at various sites. a: The presumptive adrenocortical homolog (AH) is composed of loosely-arranged cords of pale staining cells located between the posterior cardinal vein (P) and haemopoietic tissue (H). ×400. Inset: vacuolated cytoplasm (arrowheads) of cells of adrenocortical homolog. ×400. b: The corpuscle of Stannius is composed of branched cords of dark staining epithelial cells (E) separated by sinusoids (arrowhead) and is clearly delineated from the haemopoietic tissue (H) of the kidney. ×250. Inset: cells stain intensely with periodic acid-Schiff (arrows). ×560. c: The vascular poles (V) of two renal corpuscles (R) are closely apposed to the archinephric duct which has intense periodic acid- Schiff staining at the apex of its epithelium (arrowhead). Smooth muscle (M) is noted below the duct epithelium. ×400. d: A renal corpuscle showing the afferent arteriole (AA) at the vascular pole and the neck segment (NS) at the urinary pole. The columnar epithelium of the latter is continuous with the squamous cells of the parietal layer (arrowhead) of Bowman' capsule and podocytes (p) of the visceral layer overlie the glomerular capillaries (cp). ×1,000.

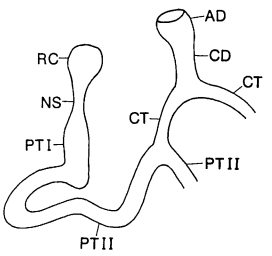

Fig. 5. Diagrammatic representation of the nephron of *Anoplarchus purpurescens* showing the renal corpuscle (RC), neck segment (NS), proximal segments I (PTI) and II (PTII), collecting tubule (CT) and duct (CD), and the archinephric duct (AD).

layer, was composed of cuboidal podocytes which were directly apposed to the capillary endothelium (Figs. 4d, 6a). Bowman's (urinary) space separated the visceral epithelium from the squamous cells of the parietal layer of the capsule, although these two layers were continuous near the vascular pole. The parietal epithelium was continuous with the epithelium of the neck segment at the urinary pole (Fig. 4d).

Tubule: As noted above, the tubular portion of the nephron consisted of a neck and two proximal segments (Fig. 5). The lumen of a single ciliated neck segment was continuous with Bowman's space at the urinary pole and there was a gradual increase in cell height from the squamous parietal cells to the ciliated low columnar cells of the neck segment (Fig. 6a). Cilia were located on the apical surface of the columnar cells and they were generally oriented downstream. A major portion of each neck cell was occupied by a large oval nucleus.

The remaining portion of the tubule was designated the proximal segment because of the characteristic brush border at the apical surface of all cells. However, two highly convoluted segments, proximal segment I and proximal segment II, were distinguished on the basis of the degree of elaboration and the staining of the brush border. Proximal segment I possessed tall columnar cells with a brush border on the apical surface with a strong positive staining with periodic acid-Schiff (Fig. 6a, b). There was almost an abrupt change from the epithelium of the neck segment to that of the proximal segment I. The cells of the latter had some apical cytoplasmic granules and vacuoles and the spherical nuclei were basally located. The change from proximal segments I to II was abrupt but it did not involve an alteration in cell height. Cells of proximal segment II surrounded a wider tubular lumen, had less intense staining of the brush border with periodic acid-Schiff, and oval nuclei in a more central or apical position (Fig. 6b).

Collecting tubule and duct: The cells of the collecting tubules and ducts had a similar morphology and they could be easily distinguished from the cells of the proximal segments by the darker staining of their cytoplasm with haematoxylin and eosin. In addition, when periodic acid-Schiff stain was used there was a strong reaction in the apical cytoplasm of cells of the collecting units (Fig. 6c). The collecting cells were low columnar, possessed oval to spherical, centrally-located nuclei, and surrounded a lumen of wide dimension. Some smooth muscle fibres were located beneath the epithelium of the collecting duct.

Archinephric duct: Throughout most of the length of each kidney there was an archinephric duct in a ventral location on either side of the posterior cardinal vein (Fig. 2c) but they united before entering the cloaca (Fig. 6c). Each duct possessed a tall columnar epithelium with ovoid or spherical nuclei. The most apical cytoplasm stained intensely positive with periodic acid-Schiff but most of the cytoplasm was pale staining (Fig. 6d). There appeared to be several layers of smooth muscle fibres beneath the epithelium (Fig. 6d).

Nephrogenic tissue: The kidneys of all animals contained clusters of cells in various stages of tubulogenesis. These cell clusters were usually in close association to the archinephric duct (Fig. 6d) and they varied in appearance from close groups of cells in a totally undifferentiated state to some in which various segments of the nephron of the collecting tubules could be visualized in early stages of differentiation. Developing renal corpuscles were also identified.

Discussion

The kidneys of *Anoplarchus purpurescens* are fused throughout much of their length and thus appear similar to those of many other marine teleosts. A clear distinction between a "head

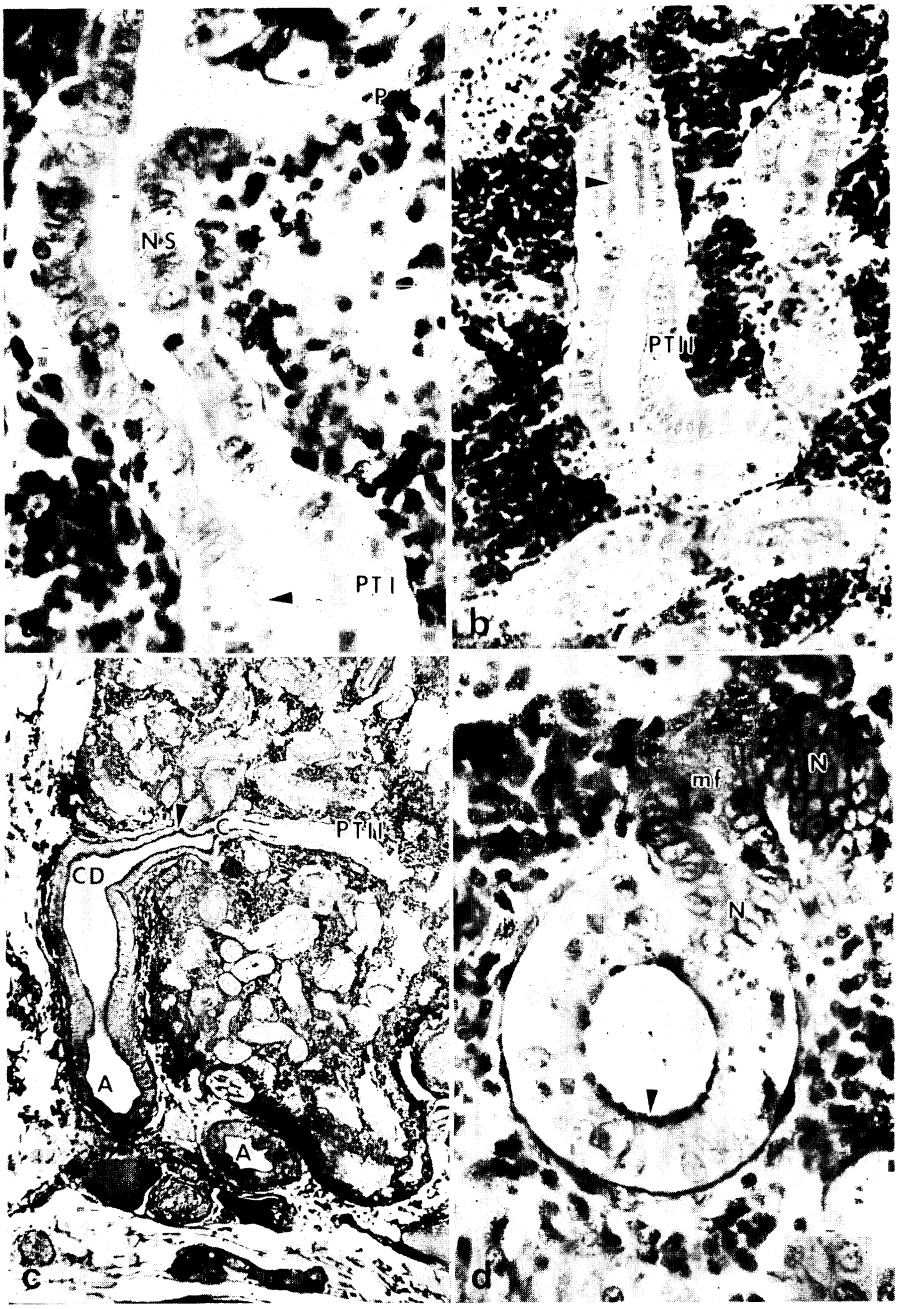

Fig. 6. Portions of the nephron stained with periodic acid-Schiff. a: A transition in epithelium is seen from the low cuboidal cells of the parietal epithelium (P) of Bowman's capsule to the low columnar ciliated cells of the neck segment (NS) to the tall columnar cells with prominent brush border (arrowhead) in proximal segment I (PTI). ×1,000. b: A proximal segment I with a thick, intensely stained brush broder (arrowhead) merges into proximal segment II (PTII) with a less conspicuous brush border. ×400. c: A proximal segment II (PTII) is continuous with a collecting tubule (C) which in turn empties into the collecting duct (CD) and lastly into the archinephric duct (A). Compare the lightly stained brush border of the proximal segment with the intensely stained apical epithelium of the collecting units (arrowhead). ×100. d: Nephrogenic tissue (N) with a mitotic figure (mf) is seemingly invaginated into the epithelium of the archinephric duct which possesses a deeply staining apical cytoplasm (arrowhead). ×10,000.

kidney" with two slender branches and a fused "trunk kidney" is characteristic of the type III kidney present in the majority of marine teleosts (Ogawa, 1962). The location of a large posterior cardinal vein within the right kidney of *A. purpurescens* also seems to be consistent with that seen in at least some teleosts (Ogawa, 1961) but, unlike Mok (1981), we are unable to suggest a phylogenetic relevance to this feature. In conformity with the structure of the kidney in other teleosts, included within the kidneys of *A. purpurescens* are presumptive adrenocortical tissue (PAT), the corpuscles of Stannius (CS), haemopoietic tissue, and renal tissue.

PAT is so designated because we did not perform the histochemical test for identification of Δ^5-3β-hydroxysteroid dehydrogenase (3β-HSD), the enzyme used as a marker of the steroidogenic nature of tissues. However, that PAT is probably the adrenocortical homolog (AH) in this species is supported by evidence of its similar location to the AH in other teleost species and by its light microscopic morphology. The distribution of the PAT cells in the most anterior region of the coelom is consistent with previous descriptions of AH in the pronephric or head kidney region in teleosts (Butler, 1973; Bhattacharyya and Butler, 1979; Oguri, 1979; Pandey, 1986). The concentration of the cells around the posterior cardinal veins conforms to the general pattern for most fishes (Kagawa and Nagahama, 1980; Yoakim and Grizzle, 1980; Youson, 1985).

CS are an endocrine tissue which exist only in the kidneys of some Holostei and Teleostei but their function is not totally understood. However, their presence is usually given more than just passing attention because of the existing belief of some role of this endocrine tissue in lowering plasma calcium ions through the secretion of a hypocalcemic hormone (Pang, 1971). The paired CS in *A. purpurescens* at the posterior end of the kidneys is a common number and location of the tissue for many teleosts (Krishnamurthy and Bern, 1969). Other features of CS in the present study which are shared in common with those in other fish species are the rich vascular supply, the surrounding and investing connective tissue, and the staining properties of the cells. The CS of *A. purpurescens* most closely resembles either the type II or type III CS described by Krishnamurthy and Bern (1969) where the investing connective tissue produces incomplete lobes and many lobules. The basophilic, basal cytoplasm reflects the extensive machinery for protein synthesis while the positive staining of the apical cytoplasm with periodic acid-Schiff is due to ubiquitous numbers of secretory granules.

The renal tissue of *A. purpurescens* is composed of marine glomerular nephrons and a collecting duct system. The possession of a neck segment, at least two proximal segments, no distal segment, and a collecting tubule has been described as typical for marine teleosts which have renal corpuscles (Hickman and Trump, 1969; Hentschel and Elger, 1987). The secretion of the divalent ions, magnesium and sulphate, is a prime responsibility of the tubule of a marine teleost (Nishimura and Imai, 1982) but the presence of glomerular filtration in the blenny gives the tubule the added responsibility of conserving filtered water, monovalent ions, and protein. All of these latter functions are likely performed in the two proximal segments. The elaborate brush border and granulated apical cytoplasm of cells in proximal segment I attest to their role in absorption of proteins which have been filtered from the plasma at the glomerulus. This segment also may be involved in the absorption of sodium and chloride ions and some water. Proximal segment II also performs these latter functions but in addition is believed to be the site where fluid and both magnesium and sulphate ions are secreted (Nishimura and Imai, 1982). The distal segment is the main diluting segment of the nephron in freshwater fishes and is apparently essential for hyperosmotic regulation. Although the distal segment is present in at least some euryhaline teleosts (Hickman and Trump, 1969; Hentschel and Elger, 1987), the absence of this segment in *A. purpurescens* reflects the fact that there is no need for dilution of urine in the hypoosmotic regulation of this marine teleost.

The role of the collecting tubule, collecting ducts and the archinephric ducts in kidney function of fishes has not been definitively established. In many cases they are considered as conduits of fully processed urine ready for release at the cloaca. However, the morphology of the ducts in some species imply that they contribute to the final composition of the urine (Youson and Butler, 1988), perhaps in the reabsorption of monovalent ions (Hickman and Trump, 1969). The presence

of mucous granules in the apical cytoplasm of the cells in the collecting tubule and duct and in the archinephric duct is a common occurrence in fishes (Bulger and Trump, 1968; Youson and McMillan, 1971; Hentschel et al., 1978; Ottosen, 1978). Undoubtedly, the intense staining of the apical cytoplasm of these portions of the kidney in *A. purpurescens* with periodic acid-Schiff is also due to the presence of mucous granules. It has been suggested that mucus may function during reproduction or in osmoregulation to acidify the urine and help in chelating specific salts to prevent the formation of potentially harmful precipitates and calculi (Dobbs and DeVries, 1975; Hentschel, 1977). Such precipitates appear to be particularly common in marine fishes where divalent ions are secreted by the tubules (Hickman and Trump, 1969; Youson, 1982).

The kidney of *A. purpurescens* showed numerous developing nephrons near the archinephric ducts. It was unclear whether these nephrons arose from previously undifferentiated nephrogenic tissue in the intertubular regions or whether they appeared as proliferating and expanding portions of existing nephrons. It is of interest that the new nephrons should appear near the archinephric duct, for this structure has been suggested as providing an inductive stimulus during early tubulogenesis (Torrey, 1965). We assumed that recruitment of nephrons reflects a continuous event which occurs during growth of the kidney.

Acknowledgments

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(Department of Zoology and Scarborough Campus, University of Toronto, West Hill, Ontario M1C 1A4, Canada)

タウエガジ科の一種 *Anoplarchus purpurescens* の腎臓，副腎およびスタニウス小体の形態

John H. Youson • David G. Butler • Kanella Tsioros

潮間帯に生息するタウエガジ科の海産硬骨魚 *Anoplarchus purpurescens* の腎臓，副腎およびスタニウス小体の形態学的研究を行った．左右1対からなる本種の腎臓は，ほぼ全長にわたって融合しており，腎臓の右側には1本の尾静脈が通っている．腎臓には腎小体が存在するが，腎尿細管には末部曲節（遠位曲尿細管）がない．尿細管は，腎小体から集合管系に合一するまでの間に，繊毛をもつ頸節と，2部よりなる基部曲節（近位曲尿細管）に分化している．集合管や尿管（前腎輸管）の細胞は特殊化し，粘液分泌作用をもつが，これは主排出管すなわち1対の原腎管の細胞である．この原腎管との密接な関係のもとに管形成が行われる．副腎相同組織が，頭腎内を走る尾静脈の周囲に存在する．一方，1対のスタニウス小体は，腎臓（体腎）後端部に局在している．上述の特徴は，すべて他の多くの海産硬骨魚の腎臓で見出されたものと一致している．